

THE MODIFICATION OF VESTIBULAR NYSTAGMUS BY
MEANS OF REPEATED ELICITATION

BY
O. H. MOWRER

A DISSERTATION

SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS
HOPKINS UNIVERSITY IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

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BALTIMORE
THE JOHNS HOPKINS PRESS
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From the Psychology Laboratory of the Johns Hopkins University

I. THE PROBLEM

The characterization of reflexes as "highly stable," "mechanically determined," "inevitable," "fixed," "predictably certain," "machine-like," and "invariable" has long been an established tradition in the biological sciences. The comparatively recent discovery that many of the so-called reflexes may be profoundly and more or less permanently modified through "practice" has therefore proved extremely disconcerting, especially to those individuals who have relied upon the "invariability" doctrine as a fundamental diagnostic implement or who have embraced it because of its pedagogical simplicity and convenience. Although experimentation has revealed that numerous other reflexes—notably, the knee-jerk, the blink, the pupillary and the post-contraction proprioceptive reactions—may be substantially altered by means of repeated elicitation under appropriately chosen experimental conditions, the most conspicuous example of susceptibility to this type of modification is afforded by the response commonly designated as *vestibular nystagmus*. Because of the particularly important diagnostic significance assigned by many otologists and neurologists to this latter response, its "functional" modifiability has been acknowledged with great reluctance; but the evidence accumulated through both controlled research and casual observation so consistently attests the validity of this phenomenon that it can no longer be either ignored or denied. A wide variety of investigations with both human and animal subjects have decisively demonstrated that this response may be strikingly reduced in both duration and magnitude by means of repeated elicitation; and any further experimental endeavor

merely to add to the already abundant evidence in this respect would be largely gratuitous. However, despite the general recognition now accorded to the reality of this phenomenon, there still exist considerable obscurity and difference of opinion regarding its probable explanation and the conditions essential for its occurrence. In view of these circumstances it is the purpose of the present study to review the various hypotheses which have previously been advanced in this connection and to attempt to determine experimentally and analytically which of them constitutes the most plausible explanation of the phenomenon in question.

II. HISTORICAL BACKGROUND

The first and, indeed, in many respects the most noteworthy attempt to give a comprehensive account of the reduction of vestibular nystagmus by means of repetition was made in 1906 by Abels (1). For many years a ship's physician, this writer became much interested in the phenomenon of seasickness, one of the most striking characteristics of which he found to be its remarkable susceptibility to "habituation" (Gewöhnung). Thus, as "anyone who has been employed at sea for some time" can readily testify, the typical symptoms of this malady usually "diminish significantly within hours or days; and on similar occasions in the future, if the interval is not too long, they do not re-appear with the same intensity. In any case, habituation is attained much more quickly in a second similar experience."

Likewise:

The facts of habituation in the case of dizziness are generally known. Learning to dance offers one of the most pertinent examples. Many people are overcome during the first attempts by violent dizziness and after-dizziness, which often last for minutes. But within a few days, and very often after a few hours in one day, these phenomena disappear entirely or virtually so. It is striking that when dancers who have already engaged in ordinary dancing [to the right] for a long time first try dancing toward the left, they generally undergo phenomena similar to, although perhaps weaker than, those incident to their first attempts at dancing. If dancing is not practiced for some time, more sensitive

individuals undergo a repetition of the same phenomena as in the beginning; only now habituation usually progresses much more rapidly than originally.

In a report published just prior to that of Abels, Ruppert (64) observed that persons much given to the popular social dances of the time were likely to show a sub-normal nystagmus when tested in a revolving chair and that this deviation from the average was usually greater for the direction of rotation most frequently involved in dancing; which latter observation, it will be noted, is strictly parallel to the observation of Abels regarding the greater immunity of dancers to the dizziness produced by rotation in the practiced than in the unpracticed direction. Feeling that it "was desirable to establish the above relationships objectively in animals," Abels performed the following experiment. Using pigeons as subjects, he placed them in a special cage which was suspended by two cords and in which the birds were free to move about. The cage and the birds could therefore be "twisted up" so that when released, they would revolve with increasing velocity until either the cords were untwisted or the cage was forcibly brought to rest by some other means.

The average rotation speed was rather considerable. The chief point stressed was to stop the apparatus suddenly after two or three dozen rotations, in order to adapt the animals especially to this act. Rotations were repeated several times a day so that every animal had to undergo in the course of the day several hundred rotations, and this was continued for several days. During this [practice period] every animal was rotated only to the right or to the left. It was thus possible to observe that the phenomena which were very violent in the beginning, when the apparatus was stopped, gradually became milder and finally were limited to a few nystagmic jerks. If now, at this stage, an animal were rotated in the unaccustomed direction, it showed, when brought to rest, the same violent phenomena as in the beginning—falling of the entire body and extremely vigorous and prolonged nystagmus. We have here the analogy of the results observed in men.

Under the conditions just described, vision was not excluded; the walls of the cage were merely of such material as "to give the

eyes of the animal the fewest possible points of fixation." Consequently,

Experiments were also undertaken in which visual perceptions were excluded. The apparatus was covered with a cloth, and an opening was left only at the top for the observation of the behavior of the pigeon. In such experiments it is known that no nystagmus is observed during rotation.¹ . . . With the stopping of rotation, however, very strong nystagmic jerks may always be observed; and it is now striking that the intensity of the jerks decreases much less during the course of days than in the animals rotated in the open apparatus, that is, the habituation, although undoubtedly present as is proved by later rotation in the unaccustomed direction, is still much less pronounced than in the first experiment.

Abels fully appreciated that any adequate explanation for the reduction of vestibular nystagmus by means of repeated elicitation must necessarily be predicated by a clear conception of the physiology of the vestibular mechanism as such; and it was largely because none of the traditional theories of vestibular functioning could be made to provide a plausible basis for such an explanation that the problem had previously "been given scarcely any attention."

A conspicuous peculiarity of the vestibular reaction system—and one which any satisfactory theory of the physiology of the vestibular mechanism must take into full account—is that a momentary or very brief angular acceleration, or retardation, elicits responses (and sensations) which usually last many times as long as the actual objective stimulus, providing that an opposing stimulus does not occur and therefore interrupt these after-effects. In the original "hydrodynamic" theory of Mach (49), Breuer (10), and Brown (12), an attempt was made to account for this striking discrepancy between the duration of vestibular stimulation and response by assuming that the angular acceleration, or retardation, produces movement of the fluids contained within the semicircular canals, which, by virtue of the inertia of

¹ The fact that this particular statement is not entirely accurate in no way invalidates the remainder or Abels' remarks.

these fluids, persists and therefore continues to elicit vestibular reactions for a considerable time after the actual, external stimulus has been withdrawn. Mach (50) shortly abandoned this explanation, however, having convinced himself through observations made with a glass model of the labyrinth that it is a physical impossibility for any fluid to "flow" within a closed system of the shape and dimensions of canals for more than a very few seconds after the cessation of either acceleration or retardation. Mach continued to regard movement of endolymph as the immediate cause of the vestibular responses produced by bodily rotation; but the prolonged persistence of these reactions he attributed to the action of a central mechanism, probably located within a sub-cortical center,² which tends to perpetuate neural conditions equivalent to those produced during actual, peripheral stimulation until either (a) there occurs an opposite type of peripheral stimulation or (b) this central mechanism is "exhausted," so to speak.

Breuer (11) acknowledged the cogency of Mach's objections to the original form of the hydrodynamic theory but refused to accept Mach's conception of a central neural mechanism as the explanation for the persistence of vestibular responses after the cessation of external stimulation. Instead, Breuer merely revised the hydrodynamic theory in such a way as to make this phenomenon dependent upon a hypothetical distortion or bending of the cupulae and attached sensory epithelia, which he assumed to be produced, to a greater or lesser degree, by any movement of endolymph, however brief, and which Breuer further assumed to persist (a) until corrected by a reverse movement of endolymph or (b) until the natural (presumably rather low-grade) elasticity of the displaced structures eventually brought them back to their normal position. Breuer (11) made a cautious attempt to apply this theory of vestibular functioning to what he himself recognized as "the great capacity for adaptation which the organ of movement-sensation certainly has."

I think it necessary now to regard it as conceivable in all these cases [of adaptation] that the elasticity of the hairs increases gradually under the influence of endolymph impacts occurring more frequently in the

² Cf. the recent histological studies of Lorente de Nó (45), (46).

generally unaccustomed direction; and, not compensated for by opposite impacts, they regain their normal position more quickly and the corresponding duration of the after-sensation of movement, i.e., dizziness, decreases.

Abels (1) criticised the plausibility of this explanation in the following words:

I must admit that it is very hard for me, and so far as I can see, also for others, to conceive how the so-called hair-cells (Hörhaare), i.e., the epithelial structures, could undergo such a change in their essential functional peculiarities in such a brief time, in the course of days or even hours. A change of this sort we are ordinarily accustomed to think of as occurring only in certain parts of the central nervous system.

On the basis of experimental evidence which cannot be pertinently described here, Abels not only refused to accept the original hydrodynamic theory as an explanation for the persistence of nystagmus and other vestibular phenomena after the cessation of external, physical stimulation but also repudiated the revised theories of both Mach and Breuer. For reasons which again cannot be given here without a long digression, Abels concluded that the prolonged after-effects of vestibular stimulation can be most satisfactorily accounted for by positing an intimate integration of both peripheral and central factors into what he termed a "sensation complex." Under the usual conditions of life—in which bodily rotations are ordinarily of brief duration and limited angular magnitude—, the central and peripheral factors comprising this "sensation complex" combine harmoniously and mutually complement each other. On the other hand, in the case of prolonged bodily rotation—where the effects of acceleration are so remote temporally from the effects of retardation that the normal occurrence of mutual interaction is prevented—disharmony develops between the various elements of the "complex" and, with sufficient repetition of this situation, the elements gradually become dissociated and the "complex" disintegrates. The reduction in nystagmus and the disappearance of dizziness are manifestations of this disintegration process.

As a possible alternative hypothesis, Abels suggested that the

reduction of nystagmus and related vestibular phenomena by means of repetition, instead of being due to a strictly pathological process, namely, the gradual breakdown of normal integration, may represent, on the other hand, a positive and useful kind of adjustment to new and unusual circumstances. This type of adjustment Abels compared to the "learning" involved in adaptation to monotonous "uniform noises, like the rippling of the brook or the ticking of a clock, which, although the impressions are always received in the same manner by the end organ, do not come into consciousness during concentrated mental activity." Although Abels appeared to regard the "dissociation" theory as by far the more satisfactory explanation of nystagmus habituation, subsequent writers in this field have been inclined, as later pages will show, to favor the "learning" hypothesis. However, the appearance of an article about to be reviewed cast so much doubt upon the actual reality of this habituation phenomenon that the problem of determining its probable explanation was scarcely so much as mentioned for more than a decade.

In a paper published in 1907, Robert Bárány (7), a Viennese otologist and later Nobel prize winner, turned his attention to the matter of nystagmus habituation. Just prior to this, Bárány (4), (5), (6) had been actively engaged in an attempt to show that the duration of post-rotational nystagmus constitutes a reliable clinical index to the functional integrity of the non-acoustic labyrinth, or vestibular apparatus; and he was therefore not slow to appreciate the bearing of Abel's experimental findings and theoretical contentions upon his own claim that vestibular nystagmus is a relatively fixed and invariable reflex in all "normal" subjects. Bárány readily admitted that Abels had unmistakably demonstrated habituation of head nystagmus in pigeons; but, says he,

We must not forget, however, that head nystagmus does not exist in men and that the results of this [Abels'] investigation are therefore not transferable to men. Consequently it was important to study the effect of habituation in men. I myself have made such a study with a single subject and for 14 days have rotated him every day 50 or 60 times in the

revolving chair. No effect upon the duration of the after-nystagmus was to be observed (7).

Bárány (7) found that professional dancers who whirl only to the right show an after-nystagmus of only about 30 seconds when passively rotated in that direction, which is considerably less than the 41-second average which he found for the same direction of rotation in a group of "normal" subjects. On the other hand, Bárány found that these same dancers showed an after-nystagmus of 49 seconds when passively rotated to the left, i.e., in the unpracticed direction, which is appreciably *above* the 39-second average of the naïve subjects for the same direction of rotation. In dancers who make a practice of whirling in both directions, Bárány found no significant variation in the after-nystagmus for either direction of passive rotation from the averages obtained from the control group.

Although practiced dancers repeatedly informed Bárány of their immunity to dizziness, he believed that this type of habituation was not accompanied—at least not in those dancers who whirl in both directions—by a corresponding reduction in nystagmus. As early as 1820, Purkinje (63) pointed out that there is always a strict correspondence between the direction, duration, and intensity of vestibular nystagmus and the direction, duration, and intensity of the visual vertigo (i.e., the illusory rotation of the environment produced by the eye movements comprising the nystagmus); and it is therefore difficult to conceive how either the nystagmus or the visual vertigo (which is presumably what Bárány meant by "dizziness" (Schwindel)) could vary to any significant extent independently of the other. Bárány summarily dismissed this difficulty, however, with the remark that "only the subjective accompaniments of nystagmus become unnoticeable, while the nystagmus itself shows no significant weakening" (7). The unreasonableness of this assumption³ (widely accepted by

³ Since the above was written, the writer has had occasion to examine a limited number of professional exhibition skaters and, also, certain members of the Monte Carlo Ballet Russe (through the courtesy of M. the Director General W. de Basil and M. the Regisseur S. Grigorieff). These individuals were asked to "spin", in characteristic manner, and permit the writer to observe their

many otologists (48), (41), (42), (51), (25)) as well as the unreliability of Bárány's experimental observations will be made manifest in subsequent pages.

So eminent was Bárány professionally and so completely did his dicta dominate otological theory and practice that only twice (to the writer's knowledge) during the decade succeeding the publication of the paper cited above (i.e., from 1907 to 1917) was the subject of nystagmus habituation referred to in the literature and then in a manner not wholly incongruent with Bárány's point of view. Thus, in 1909, Wintermute (65) wrote as follows:

In testing a person who, by occupation, is constantly revolving in one direction, the normal reactions will not hold. Ballet dancers who whirl only in one direction, which is the rule, show great difference in the resulting nystagmus when turned to the right and left. When

eyes immediately afterwards. In many cases, there was no detectable post-rotational nystagmus whatever. In certain other cases, a noticeable (though distinctly "sub-normal") nystagmus was present, in which event a concomitant visual vertigo was also present, except in one subject, Miss Nellie Prantell of the New York Skating Club. Miss Prantell showed a nystagmus subsequent to whirling of 5 to 8 seconds' duration but insisted that she experienced no illusory movement of the visual environment under these circumstances. This remarkable testimony suggests that the assumption of Bárány cited above may, in exceptional instances, be valid; that is to say, it is not wholly improbable that an occasional individual may learn to interpret the visual consequences of post-rotational nystagmus in such a manner as to eliminate the apparent movement of the environment. This, however, is a matter which will need to be subjected to a careful experimental analysis before a final conclusion may be reached.

In this connection it is perhaps pertinent to call attention to a statement by Holsopple (37) to the effect that in some individuals the nystagmus produced by passive bodily rotation may be greatly reduced in duration by means of repetition without the duration of the post-rotational illusion of bodily turning (which characteristically appears if the eyes are kept closed) seeming to be in anyway affected. Here would appear to be a situation somewhat analogous to that hypothesized by Bárány. However, since it has been repeatedly demonstrated that post-rotational nystagmus ordinarily lasts much longer when vision is excluded than when vision is permitted (58) and since Holsopple tested the duration of the post-rotational nystagmus of his subjects with their eyes *open* and the duration of the post-rotational illusion of bodily turning with the eyes of his subjects *closed*, there is some reason to suppose that in the latter situation the nystagmus may have regularly lasted quite as long as the illusion of turning. Here, again, further experimental inquiry is obviously needed.

turned in the direction in which they are used to revolving the nystagmus is very small, as a consequence of their continual practice.⁴

Then in 1914 Güttich (34) reported that repeated administration of the Bárány rotation test usually results in a marked decrease in the duration of the nystagmus thereby elicited. However, this writer was inclined to attribute this diminution of nystagmus to a decline in the general nervous tension and hyperirritability which subjects usually manifest during the first few administrations of the test, rather than to any real reduction in the strength of the reflex. Although Güttich's observations are thus opposed to the experimental results reported by Bárány, this writer does not, however, voice any objection to Bárány's assumption that vestibular nystagmus is fundamentally fixed and invariable.

III. THE MINEOLA CONTROVERSY

For several months prior to the United States' entrance into the World War in 1917, it appears that a group of American otologists "had been in correspondence with the Medical Department of the United States Army upon the subject of the physical requirements of applicants for the flying forces" (51) and had convinced the medical officials that "by demonstrating an actively normal organ of equilibrium in every prospective aviator, this Government will avoid many costly accidents in the air which otherwise would be avoidable" (3). The result was that when war was actually declared, this same group of otologists was put in charge of special clinics in "each of 35 cities throughout the United States . . . for the examination of candidates for the aviation service" (42), and in these clinics the Bárány rotation test made the almost exclusive basis for the determination of specific flying ability. In fact, this test was regarded by the otologists and certain army officials as having such high diagnostic value in this connection that during the first few weeks of

⁴ Although Wintermute speaks as if these observations might have been original, it seems not unlikely that he merely borrowed them from Bárány, whom he cites as authority for numerous other statements.

America's participation in the war, "there was no medical examination—beyond a rotation test—before a man began flying" (2).

The great importance thus attached to the rotation test seems to have involved two major fallacies. In the first place, there was apparently a gross over-emphasis upon the rôle of the vestibular mechanism in flying. This, however, has been considered in another connection (55) and need not be further discussed at this time.

The other fallacy—and the one of greater significance for the present discussion—was the illicit inference that since all individuals with demonstrably pathological non-acoustic labyrinths show unusual reactions to bodily rotation, then all individuals who show unusual reactions to bodily rotation must, ergo, have pathological labyrinths. Thus to quote:

We start out with a fixed and definite idea that a normal internal ear, intact nerve pathways leading to normal centers, will *invariably* produce a rhythmic nystagmus and vertigo when a stimulus is applied. . . . If, on the other hand, stimulation of the internal ear fails to produce one or all of these responses, the evidence points positively to an impairment at some point of this apparatus (24).

However, some months after the otologists, wholly oblivious of the clinical as well as experimental observations reviewed in the preceding section of this paper, had been put in charge of the selection of candidates for the air service and several hundred men had been barred from entering and some men already having brilliant flying records actually ejected from the service on the basis of the above-mentioned test, serious misgivings began to arise in certain quarters as to whether this test could invariably be relied upon to test what it was supposed to test, namely, the normality or abnormality of the non-acoustic labyrinth.

Suspecting that the veteran aviators who had been tested by the otologists and barred from further service because of sub-normal nystagmus had acquired this peculiarity of response as a result of the repeated bodily rotation to which they had been subjected in connection with "stunt" and "combat" flying, Major Knight Dunlap, then head of the Department of Psychol-

ogy of the Medical Research Laboratory at Mineola, Long Island, detailed Captain George Wells, in May, 1918, to obtain the post-rotational nystagmus time of a group of professional acrobats and whirling dancers in New York City. That the results, whatever they might be, could not be discredited by a charge of incompetency on the part of the examiner was assured in advance by having the tests actually administered by an army otologist who had expressed his willingness to co-operate in this enterprise. The data thus obtained, which were carefully scrutinized by Major Dunlap and others, showed that these New York subjects (in whom a perfect sense of balance was obviously imperative for professional proficiency) had, in almost every case, a nystagmus time far below the minimum (16 seconds) set by the otologists for admission into, or continuation in, the air service. In fact, so strikingly did these findings confirm the supposition that repeated bodily rotation may reduce nystagmus that they were taken in charge by a medical officer and suppressed. Certain data, published later and purporting to be the nystagmus measurements of a group of acrobats and dancers whose initials were those of the group measured under Captain Wells' supervision, are not, however, the data for these individuals.⁵

Parsons and Segar (60), Fridenberg (27), and a few other writers were inclined at this time to agree with Major Dunlap and his colleagues that "trapeze performers and Russian dancers have very little, if any, nystagmus after whirling" and that "men who have a so-called 'normal' nystagmus time before flying often lose all or a great part of it after numerous flights" (60). However, the majority of the army otologists persisted in their contention that nystagmus habituation does not occur as a result of repeated bodily turning. Thus, Jones (42) emphatically declared that "All experienced aviators that have been examined have, without exception, shown normal responses in the turning-chair." Likewise, Fisher and Babcock (26) wished to "have it definitely settled once and for all that army aviators do not lose

⁵ Statements occurring in this section which are not otherwise documented are based upon information obtained by the writer directly from Professor Dunlap.

their nystagmus as a result of the rotation and whirling to which they are subjected."

In the hope of bringing this controversy to an end, Major Dunlap, commissioned Captain Madison Bentley to begin an experiment at the Mineola laboratory, on June 6, 1918, with six enlisted men as subjects (51). Each man was subjected to a schedule of daily rotation which consisted of five periods of clockwise rotation, each period comprised of ten turns at the rate of approximately one revolution in two seconds, followed by five similar periods of rotation in the opposite direction. The successive periods of rotation were separated by rest intervals of about two minutes; the rotation was done by hand, with the subject sitting upright in a specially constructed revolving chair. In all, one hundred revolutions, fifty in one direction and fifty in the other, were given to each subject daily. The following table shows the reduction in the nystagmus time of each of the six subjects during the first ten days of the experiment.⁶

SUBJECTS	ORIGINAL TIME	FINAL TIME	REDUCTION
	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>
A	30	12	18
B	27	10	17
C	26	11	15
R	21	14	7
S	25	8	17
W	28	15	13

The results of this experiment aroused a storm of protests and objections on the part of the otologists; abnormality of subjects and incompetence on the part of the experimenters were advanced as possible explanations of these findings, and even insinuations regarding the scientific integrity of those in charge of the project were made. In September of the same year (1918), the otologists, hoping to obtain different results, initiated an experiment similar to the one conducted by the psychologists. They used ten adult subjects and about the same schedule and method of rotation.

⁶ The experiment was continued for an additional ten days with a still further, though relatively less conspicuous, decline in the nystagmus of the six subjects.

This experiment was reported to have been continued for nine weeks, at the end of which time it was admitted that there had been a reduction in the duration of the post-rotational nystagmus "in some cases"; but it was insisted that this reduction merely represented an "increased control of the voluntary eye movements" and was "in no sense the result of changing character or intensity of the vestibular stimulus" (2). This latter remark is, of course, quite beside the point; so far as the writer is aware, no one had previously suggested that the repeated rotation involved in the habituation of nystagmus alters either the "character or the intensity of the vestibular stimulus." The real point at issue was whether repeated bodily rotation does or does not tend to reduce the duration of the nystagmic *responses*; and the otologists themselves, despite their best efforts to the contrary, had confirmed the contention that such a reduction does occur under these conditions.

That "increased control of the voluntary eye movements," i.e., greater facility in "voluntary fixation of the gaze," may have been to some extent responsible for the decrease in the duration of post-rotational nystagmus observed both by the psychologists and the otologists is not entirely improbable; but, for reasons clearly stated by Griffith (32), this could not have been the only explanation for the observed effect. Moreover, it has subsequently been demonstrated that nystagmus habituation may occur when the subject is practiced with vision entirely excluded, that is to say, under conditions in which fixation is impossible and the "control of the voluntary eye movements" otherwise extremely difficult.

Major Dunlap, on the other hand, refrained at this time from advancing any particular explanation for the reduction of nystagmus produced by repeated bodily rotation. He summarized his position in the following words.

Repetition of turning certainly leads, under certain circumstances, to a decrease in after-nystagmus. But that the decline depends in any fixed way upon the length of the temporal interval can not be maintained upon the basis of the evidence at hand [Cf. Holsopple (38)]. The decline is not to be laid to a simple process of adaptation in the receptor

organs of the labyrinth, for such sensory adaptations as are best known—visual, tactual, and thermal—are of brief duration, and furthermore, they rapidly disappear with the lapse of stimulation. Still less is the effect of repetition to be disposed of as a case of ‘fatigue,’ a term which the uncritical lay reader might readily suggest. Nothing like fatigue (used in the sense of waste products and lowered metabolism) is here observed; and the proposal of that term as an hypothesis would be a loose use of the argument from analogy, which explains nothing. If genuine fatigue were actually induced by rotation, its effects would scarcely remain unmodified for four or five days. The explanation of the observed decline in nystagmus remains, therefore, for further experimentation made under more favorable technical conditions than the department [of psychology at Mineola] has been able to command (51).

IV. SUBSEQUENT EXPERIMENTATION

The controversy between the army otologists and psychologists at the Mineola Laboratory, which has been discussed in the preceding section, naturally had numerous *post bellum* echoes and stimulated a variety of experimental studies. These studies, which have been reviewed by Griffith (32), (33), Holsopple (36), (37), and others, will, however, be mentioned here only in the most cursory manner.

Griffith (29) subjected sixteen college students to a program of repeated daily rotation, thereby reducing the average nystagmus time of the group 79 per cent. This writer gives the following summary of his results.

We have found that, as turning is repeated from day to day, the duration of the after-nystagmus, the number of ocular movements made, and the duration of the apparent movement [visual vertigo] rapidly decrease. The major part of this decrease occurs within the first few days. The decrease takes place not only from day to day but also within a period of ten trials on any single day. The amplitude of the ocular movements and the number of movements made per second also decrease as repetitions increase.

Griffith, who also reported strictly analogous results from the repeated rotation of white rats (30), made no attempt to offer an explanation for the reduction of vestibular nystagmus by means

of repeated elicitation other than to suggest that "a 'nystagmus curve' is quite comparable with the common 'learning curve,' save for the absence of plateaus."⁷

Dodge (14) suggested that it was "conceivable that the decrease of nystagmus which he [Griffith] observed was really an increased control of eye-movements by visual fixation" (which, it will be recalled, is the hypothesis that had been advanced by the army otologists (2)). Dodge subjected himself to an intensive schedule of repeated bodily rotation under conditions in which the possibility of visual fixation could be controlled and the nystagmic responses graphically recorded. The results obtained by Dodge in his experiment "furnish striking and complete confirmation of Griffith's results together with important additional data." Of these latter perhaps the most significant is the finding that repeated rotation in only one direction decreases the after-nystagmus produced by rotation in this direction about twice as much as it decreases the after-nystagmus for the unaccustomed direction.⁸

On the basis of his experimental data, Dodge concluded that nystagmus habituation is probably a form of "learning," comparable to or perhaps identical with the learning displayed by human beings and other animals in the gradual abandonment of responses found to be useless or actually harmful under the circumstances in which most frequently elicited. A rat learns

⁷ In a later publication (32), Griffith remarks that: "Numerous observers have reported the course of the recovery that takes place in animals after surgical means of exciting the canals have been resorted to. In most cases the recovery (indicated by the disappearance of unusual movements) has been far more rapid than the healing of the wound. It is curious that this fact did not suggest that continued excitation of the canals (which in the case of a wound to the canals would seem to be the case) might lead to a profound modification of the effects of ampullar stimulation." Whether the process involved in recovery after mechanical disturbance of or injury to the semicircular canals is the same as that involved in the reduction of nystagmus by means of repeated elicitation is a question which cannot be definitely answered at the present time. On a subsequent page certain experimental evidence will be cited, however, which points to a distinct difference in this respect rather than to an identity such as Griffith's comments suggest.

⁸ Cf. the observations of Bárány (7) and Wintermute (65) regarding the nystagmus of dancers who turn only in one direction and the experimental results of Abels (1) with pigeons as subjects.

to avoid a cul-de-sac in a maze. "Unless the ocular compensation [nystagmus] is useful, it simply dies out. Why not?" During bodily rotation, nystagmus is highly useful in that it automatically facilitates efficient vision; during the post-rotational period, on the other hand, nystagmus is distinctly disadvantageous in that it distorts vision and makes for spatial disorientation. (Perhaps here is one explanation for the greater reduction of the after-nystagmus for the practiced than for the unpracticed direction of rotation.) This theory that nystagmus habituation may represent an adaptive, learning process, which was certainly anticipated by Abels (1) although not so explicitly stated by him as by Dodge, will be referred to again on a later page.

Holsopple (36) confirmed with human subjects the finding of Dodge (14) and others (1), (65), (7) that repeated rotation in one direction significantly diminishes the duration of the nystagmus produced by this type of stimulation but does not equally diminish the nystagmus elicited by rotation in the opposite (unpracticed) direction; and he likewise verified the observation of other investigators (43), (14), (1) that the presence of vision and the consequent possibility of fixation are not essential for the occurrence of nystagmus habituation. (Using rabbits as subjects, Maxwell and Pilz (54) have shown, in fact, that nystagmus habituation proceeds more rapidly when vision is excluded than when it is permitted.)

In a later publication, Holsopple (38) has demonstrated that the unequal reduction of after-nystagmus for the clockwise and counter-clockwise directions of rotation produced by repeated rotation in only one of these directions is probably not dependent (providing vision is excluded) upon the direction of the repeated rotation but rather upon the difference in the duration of the successive rotation (acceleration-to-retardation) and rest (retardation-to-acceleration) intervals comprising the practice schedule (Cf. Dunlap (51)). For example, if the rotation interval is relatively brief, say 10 seconds, and the rest interval relatively long, say 50 seconds, the after-nystagmus produced by rotation in the direction of practice will be more markedly reduced than the after-nystagmus produced by rotation in the opposite direc-

tion. On the other hand, if the rotation interval is relatively long, say 50 seconds, and the rest interval is relatively brief, say 10 seconds, the after-nystagmus produced by rotation in the direction of practice will be *less* markedly reduced than the after-nystagmus produced by rotation in the opposite direction. Thus, "Either type of nystagmus can be reduced by rotation in either direction depending on the distribution of time allotted to rotation and rest intervals" (38).

This discovery led Holsopple to posit the theory that "Nystagmus time decreases by virtue of having frequently run to normal completion and is *not* reduced merely because of the frequent occurrence of its stimulus." Although useful as a description of the conditions under which nystagmus habituation is most likely to occur, this statement, it should be noted, can scarcely be said to constitute an explanation of why the habituation actually occurs.

Maxwell, Burke, and Reston (52) have reported that, in rabbits, nystagmus habituation proceeds less rapidly, other conditions remaining constant, when the head is held in a fixed position with reference to the rest of the body during the rotation practice than when the head is left free. This finding was verified in an experiment by Lumpkin (47) with the same type of subject, but was contradicted by results obtained by Dorcus (15) from human subjects and by King (43) from pigeons. Whether there is thus a real difference in the way different types of subjects react to head fixation during repeated bodily rotation or whether the reported discrepancy is merely an artifact resulting from the limited number of subjects used will have to be determined by further experimentation.

Hoshino (39) has advanced the theory that the reduction of nystagmus occurring with repeated bodily rotation is due merely to fatigue, and has based this contention upon the fact that in rabbits whose nystagmus had been reduced by a single session of repeated rotation he found a considerable degree of recovery after a few hours' rest. That this recovery was probably not complete and that the effects of the one session would have summated with the effects of subsequent sessions are facts which

Hoshino entirely neglected and which are quite inconsistent with the fatigue hypothesis suggested by him.

In an experiment reported by Maxwell (55) and again in a study by Pilz (61), it was found that not only is the after-nystagmus of rabbits reduced by repeated bodily rotation but that the nystagmus occurring during rotation is also diminished, although less decidedly. "At a time when the after-nystagmus had practically disappeared, the rotation-nystagmus had not usually been reduced as much as 50 per cent. Indeed it is doubtful if the rotation-nystagmus would ever disappear under the conditions of these experiments" (53). This difference in the extent of habituation shown by the rotation and the post-rotation nystagmus may have been due to the fact that, under the conditions of the experiments just cited, the vestibular nystagmus occurring during rotation was reinforced by the movement of the visual environment in relation to the subject, whereas the vestibular nystagmus occurring during the period following rotation tended to be inhibited by the visual stimulation arising from the environment, which at this time was of course stationary with reference to the subject. In keeping with the theory that nystagmus habituation is an adaptive process, it would naturally be expected, therefore, that the post-rotational nystagmus would be more significantly modified. Or again, it may have been that the successive periods of rotation were considerably briefer than the interpolated rest periods, under which conditions, according to Holsopple's hypothesis, the post-rotational nystagmus would have been more decidedly reduced than the rotation nystagmus, quite irrespective of the visual factors. Unfortunately, neither Maxwell nor Pilz described the experimental conditions under which their respective investigations were conducted in sufficient detail to make it possible to determine whether the visual or the temporal factors (or both) were responsible for the results obtained.

Fearing (21) and King (43) have found that the nystagmus resulting from a given rotational stimulus is more prolonged in young pigeons than in older birds; but Huddleston (40) has reported exactly the opposite. Huddleston and King are agreed, however, that the nystagmus of squabs is more readily

habituated than the nystagmus of adult pigeons. King suggested that the lower susceptibility of adult birds to experimental nystagmus habituation may indicate that the repeated circling and turning involved in flying has already produced a certain amount of habituation and has therefore rendered the older birds relatively immune to further effects of this kind; but this hypothesis presupposes that adult birds actually show a significantly briefer nystagmus than do young birds, which assumption Huddleston has explicitly contradicted. It seems probable to the writer that the greater susceptibility of young birds to nystagmus habituation, if it indeed exists, is merely a manifestation of the greater adaptability and flexibility of behavior which is characteristic of all young animals.

King (43) has further reported that decerebrate (and therefore psychically blind) squabs are quite as susceptible to nystagmus reduction by means of repeated bodily rotation as are blinded but otherwise normal squabs. On the basis of this finding, King concluded that nystagmus habituation "is not of the nature of a learning process." This inference is of course based upon the assumption that learning can occur only in the cerebral hemispheres, a contention which Beritoff (8) has disproved by showing that conditioned responses may be established in entirely decerebrate pigeons. Moreover, the neurological relationship between the vestibular apparatus and the brain is such as to make the cerebellum or the brain-stem a more natural and more logical place than the cerebrum for the occurrence of whatever neural changes are involved in nystagmus habituation.⁹

⁹ Henri and Stodel (35) have reported that the torsion of the head produced in frogs by unilateral labyrinthectomy usually disappears in about six weeks. If, however, at the end of this time, the animal is decerebrated, the original symptoms reappear and persist as long as the animal lives. Moreover, if the animal is decerebrated first and its labyrinth removed later, there is never any perceptible recovery from the effects of the latter operation. Although Henri and Stodel employed frogs as subjects in their experiments and King used pigeons, the facts revealed in these two investigations are presumptive evidence in favor of the suggestion advanced by the present writer in Note 7 that the process responsible for recovery from the effects of labyrinthine operations may be fundamentally different from the process involved in the habituation of nystagmus by means of repetition.

That the reduction of nystagmus by means of repeated elicitation is dependent upon some sort of change occurring somewhere within the central nervous system—rather than upon injury to or structural modification of the vestibular receptor mechanism—is clearly shown by investigations reported by Maxwell, Burke, and Reston (52), Gould (28), Detlefson (13), Dunlap (20), and Fearing and Mowrer (22). However, these studies have been discussed in two other papers (22), (59) and will not be further reviewed in the present report.¹⁰

Of the various investigators who have studied the effect of repeated elicitation upon the duration of vestibular nystagmus, three have reported negative findings. The first of these investigators was Prince (62), who described his experiment, in part, as follows:

Cats were subjected to interrupted horizontal rotation over a prolonged period and the nystagmus time observed. The rotation tests (20 turns in 20 seconds) were applied 50 to 60 times daily at intervals of two minutes and were repeated for twenty consecutive days.

The duration of post-rotation nystagmus under these conditions was found to vary slightly in different animals. With 20 revolutions in 20 seconds the maximal variations in the post-rotatory nystagmus times observed in six animals were from 12 to 19 seconds.

By way of summary, Prince remarks that:

The ocular responses to rotation for each animal remained fixed within narrow limits and were unaffected by prolonged rotation. It may be concluded therefore that rotation tests give an adequate index to labyrinth activity.

Whether the cat is in some way unique or whether the conditions of Prince's experiment varied in some subtle but significant way from the conditions of similar experiments with other types of subjects cannot at present be determined. The need of further

¹⁰ The effect of *continuous* rotation upon the bodily equilibrium of rats has been studied by Griffith (31) and by Dorcus (16). However, since the findings of these experimenters have only an indirect bearing upon the present discussion, they will not be reviewed here. For a discussion of the results obtained from these investigations, see Mowrer (59).

studies of nystagmus habituation with feline subjects is clearly indicated.

Although concerned with the problem of habituation in only an incidental manner, Borries (9) has reported that in pigeons "Several rotations after each other did not influence the post-rotatory nystagmus." The statements of numerous other investigators, who have also studied the effects of repeated bodily rotation in pigeons and whose findings have already been referred to, suggest that Borries' observations must either have been inaccurate or else the conditions of his experiment must have varied in some manner not indicated in his report from the experimental conditions used by other investigators.

Dorcus (17) has recently reported an experiment in which two litters of white rats (eight in all) were born and reared to the age of three months in a large cylindrical cage ($3\frac{1}{2}$ ft. in diameter). During the entire period of the experiment, this cage was intermittently rotated by a motor which was automatically started and stopped by a specially designed clock commutator. Each period of rotation lasted for half an hour and was followed by a rest period of one and one-half hours. The rotation was exclusively clockwise and at the rate of one revolution per second. Two weeks after the intermittent rotation had ended, Dorcus immobilized the eight rats and subjected each of them to a twenty-second period of clockwise and an equal period of counter-clockwise rotation at the rate of one revolution in two seconds. On the average, these animals showed a post-rotational nystagmus for both directions slightly (though probably not significantly) higher than that reported by Griffith (30) for a group of rats not previously subjected to any passive bodily rotation whatsoever.

In order to account for this unexpected finding, Dorcus tentatively advanced the suggestion "that marked reduction does not occur in animals unless they are kept in a more or less fixed bodily position [during the practice rotation]." It is true that the majority of experimenters who have previously reported marked nystagmus habituation have immobilized their subjects during both the practice and test rotations. Abels (1) and Griffith (3), however, are exceptions in that they allowed their subjects

(pigeons and rats, respectively) complete freedom within a small cage during all periods of rotation; and, it will be recalled, both of these investigators reported virtually complete abolition of the nystagmus of their subjects. Since Dorcus' rats were practiced under rotational conditions somewhat dissimilar to those employed in the subsequent nystagmus test, it is possible that some variation between the two sets of conditions—for example, difference in the duration or velocity of rotation or in the rate of acceleration and retardation—may have been responsible for the observed absence of the habituation effect.¹¹ Or, again, it may have been that the post-rotational nystagmus shown by Dorcus' subjects under the test conditions was increased, and the habituation effect of the previous rotation therefore masked, by the fact that these animals were unaccustomed to being handled or immobilized and were consequently probably highly excited and unusually responsive. Such an explanation is at least suggested by the finding, recently reported by the writer (56), that both naïve and habituated pigeons usually show a considerably longer post-rotational nystagmus when tested immediately after being handled and excited than when hooded and immobilized and allowed to remain undisturbed in a quiet room for twenty minutes before being tested.

Although the negative findings of Prince, Borries, and Dorcus, which have been discussed in the immediately preceding pages, do not in any sense prove that vestibular nystagmus may not, under certain conditions, be considerably reduced or even abolished by repeated elicitation, they do, however, clearly show that this response is not *invariably* diminished by repetition. More complete information than is now available regarding the particular circumstances under which nystagmus reduction does and does not occur is therefore obviously needed before any definite conclusion may be drawn regarding the exact nature of the

¹¹ Griffith (30) has remarked in this connection that "It must be emphasized that any decrease [in the post-rotational nystagmus times of rats] is for one set of conditions only. . . . Changing the speed or the number of rotations at any time produced a similar reappearance of nystagmus, but never in its original intensity or temporal duration."

process specifically responsible for this type of response modification.¹²

V. PROCEDURE AND RESULTS

The experiments reviewed in the preceding sections of this paper indicate that a variety of factors—presence or absence of vision, direction of rotation, emotional disturbance, relative duration of the successive rotation and rest intervals, fixation or non-fixation of the head, age and type of subject, etc.,—may be influential in determining the rate and extent of the nystagmus reduction produced by any given schedule of repeated bodily rotation. It is not surprising, therefore, that the results reported by different investigators have frequently involved apparent contradictions and inconsistencies. No less understandable is the lack of agreement existing among the various writers regarding the probable explanation of nystagmus habituation. In the hope of somewhat clarifying rather than merely increasing this confusion, the writer has undertaken a series of habituation experiments in which an attempt has been made to hold constant all conceivably significant factors, except some single factor which is varied, in each experiment, in a controlled manner. The writer readily concedes that the results obtained from the present investigation still leave unsolved many of the problems discussed in the foregoing pages, although perhaps certain questions have been answered with a fair degree of finality and a few previously unanticipated facts brought to light.

The rotation apparatus used in the present investigation is pictured in plate 1. The *driving unit* is merely a modified form of the device previously described by Dunlap (19) and will not be discussed here except to mention that the starting and stopping of the rotation unit were accomplished by the use of electro-

¹² In a recent publication, Lorente de Nó (44) has briefly discussed nystagmus habituation and has referred to experimental results reported in two earlier papers (one by himself and the other by A. Malan), which, however, have not been accessible to the writer and for this reason are not cited in the present review. Fischer (23) has also alluded to this topic, with the comment that the process involved in nystagmus habituation is probably a "central phenomenon," but has presented no original experimental data.

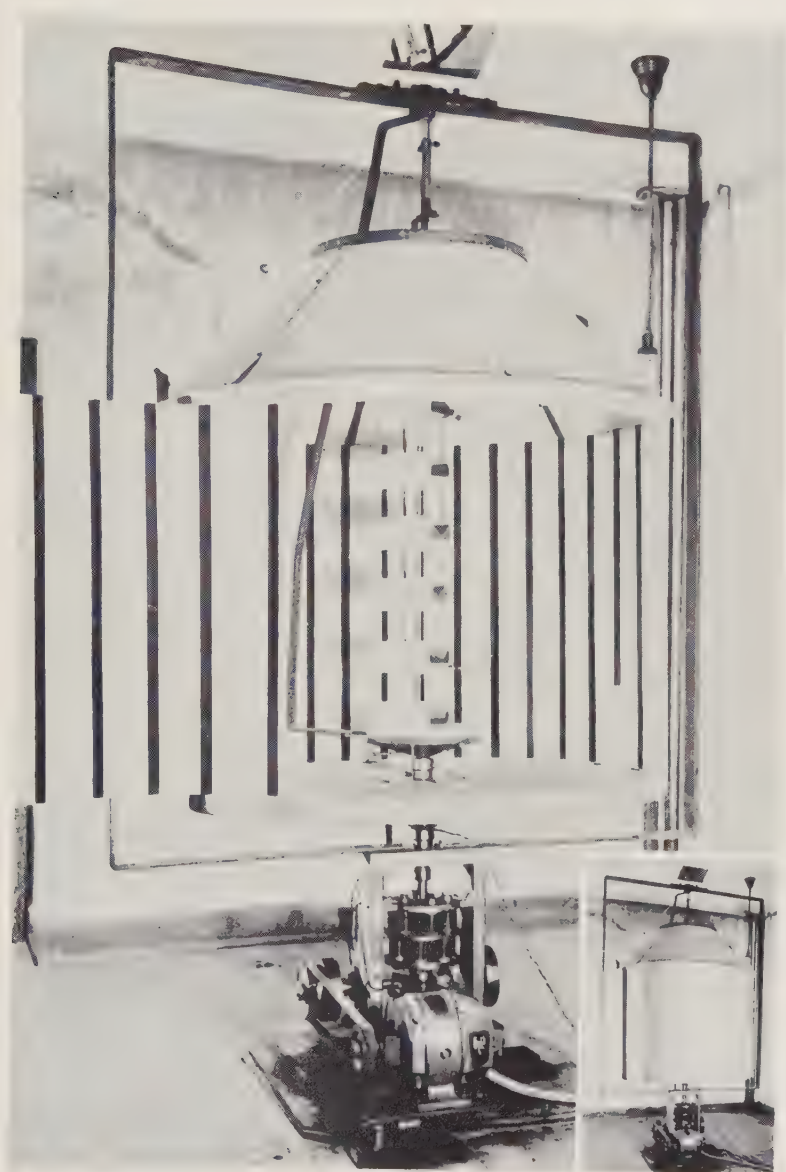


PLATE 1

magnetic clutches rather than by merely starting and stopping the electric motor. The *rotation unit* consisted of two distinct parts: (a) a large cylinder four feet in diameter and approximately four feet high and (b) a multiple holder capable of accommodating six subjects simultaneously (see plate 2). The cylinder and the holder could each be rotated in either direction with the other at rest, or both could be rotated together in either direction. The light gray interior of the cylinder was well illuminated and was variegated by vertical black stripes one inch wide and four inches apart. Whenever the cylinder was rotated alone or in conjunction with the holder, the door in the side of the cylinder was closed, as shown in the insert in the lower right-hand corner of plate 1, and all visual stimulation from the experimental room thereby excluded save for an insignificant amount of light entering the cylinder from the relatively small opening in the top of the conical cover. A mirror placed at a suitable angle about eighteen inches above this opening made it possible for the experimenter to observe the subjects at all times under these conditions. A clamp, suitable for holding a 16 mm. motion picture camera was mounted immediately above the cylinder and was articulated with the platform, upon which the multiple holder was fastened, in such a way as to cause the camera to rotate concurrently with the platform, or, if the platform were at rest, to remain at rest, uninfluenced by movement of the cylinder. (When motion pictures were to be made, the multiple holder was replaced by a holder accommodating a single subject.)

Partly because of the frequent use made of them in previous studies of this kind and partly because of other reasons, such as convenience in keeping and handling, pigeons were selected as subjects for this investigation. Common adult birds were used in all of the experiments and, when not being actually experimented with, were kept in a large outdoor cage which provided an opportunity for abundant exercise and generally healthful living conditions.

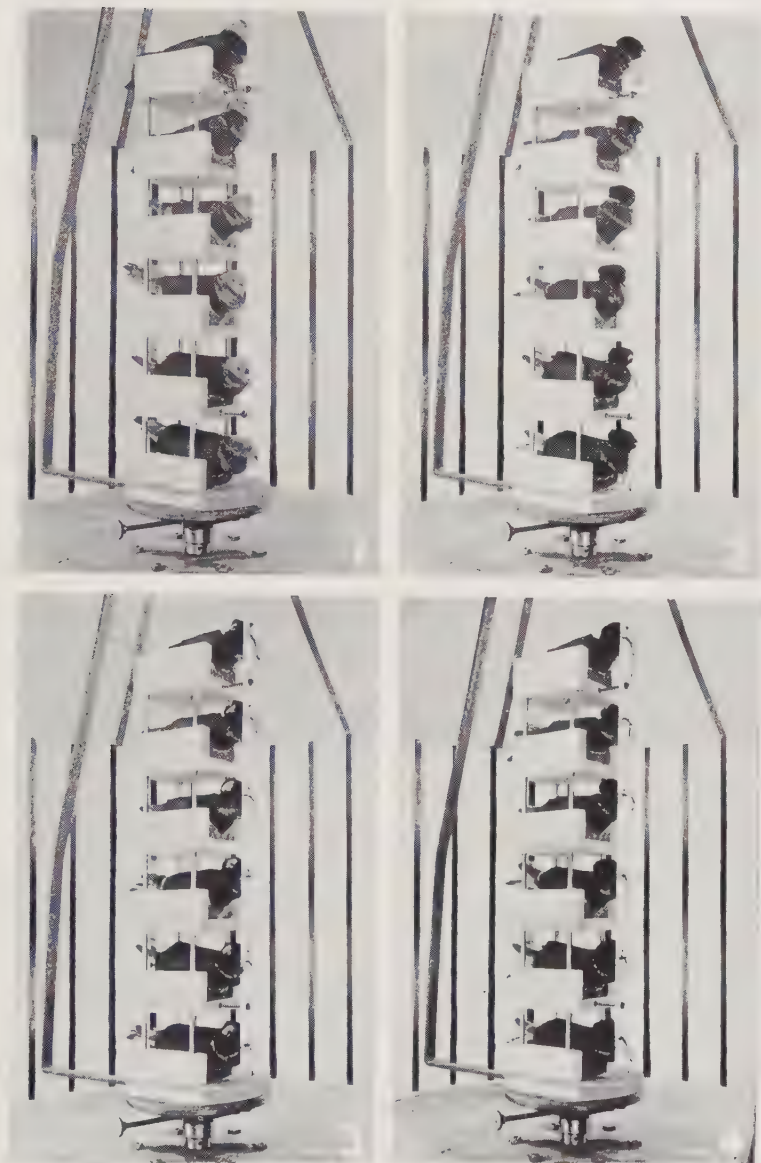


PLATE 2

Series A

The first series of experiments, undertaken primarily as a preliminary study, was commenced on March 9 and involved the use of twenty-four subjects. On this date each bird was given a standard test for vestibular nystagmus for both the clockwise and counter-clockwise directions. The clockwise and the counter-clockwise rotation periods both consisted of fifteen turns in thirty seconds and were separated, for each bird, by approximately half an hour; acceleration and retardation each occupied about 0.5 seconds for both directions of rotation. The post-rotational nystagmus, which was recorded with a split-second stop-watch, was timed from the onset of retardation to the last nystagmic head movement. The nystagmus times obtained from the twenty-four subjects for the clockwise and counter-clockwise directions of turning are given in appropriately designated columns in table 1.

The birds were then divided by random selection into eight groups of three birds each. Beginning on March 10, each of these groups was subjected to a schedule of repeated daily rotation under the various conditions indicated by the legends in the two columns at the left in table 1. Each daily experimental session consisted of six periods of rotation, each period being comprised of fifteen turns in thirty seconds with interpolated rest period of equal duration.

At the end of 32 days, the habituation routine was discontinued; and each bird was tested for post-rotational vestibular nystagmus in exactly the same manner as before the habituation was commenced. The nystagmus times thus obtained for each of the 24 birds for the clockwise and counter-clockwise directions are given in table 1. In the two extreme right-hand columns of table 1 are also given the *percentage* of change between the original and final post-rotational nystagmus time of each bird for both the clockwise and counter-clockwise directions. The plus (+) or minus (−) sign in front of each entry in these two columns indicates whether this change was of the nature of an increase or a decrease.

It is apparent from the results thus represented in table 1 that the most striking reduction in vestibular nystagmus was produced

TABLE 1

Original and final post-rotational nystagmus times of 24 pigeons and percentage of change produced by 32 days of habituation to various conditions of rotation

		GROUP	MARCH 9		APRIL 11		CHANGE	
			CW	CCW	CW	CCW	CW	CCW
			<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>per cent.</i>	<i>per cent.</i>
Rotation of body only. Vision excluded	Rotation alternately clockwise and counter-clockwise	1	24.8	20.6	4.2	5.6	-83	-73
			24.8	28.8	11.2	12.2	-55	-58
			24.8	25.0	11.2	10.6	-35	-58
			Average.				-64	-63
	Rotation in clockwise direction only	2	28.0	24.2	8.6	8.8	-69	-64
			22.8	20.4	7.6	7.4	-67	-64
27.2			32.2	15.4	11.2	-44	-65	
Average.				-60	-64			
Rotation of body only. Vision permitted	Rotation alternately clockwise and counter-clockwise	3	22.4	21.6	17.6	20.8	-22	-04
			26.4	19.2	21.8	19.6	-17	+02
			27.0	21.2	22.4	23.4	-17	+10
			Average.				-19	+03
	Rotation in clockwise direction only	4	31.0	27.8	26.8	18.8	-14	-32
			19.0	20.2	30.1	21.6	+58	+07
27.4			25.0	33.6	24.8	+23	-01	
Average.				+22	-09			
Rotation of body and environment	Rotation alternately clockwise and counter-clockwise	5	19.0	19.6	10.4	10.0	-45	-49
			17.0	18.6	12.0	8.2	-29	-50
			35.0	24.6	29.8	20.6	-14	-16
			Average.				-29	-38
	Rotation in clockwise direction only	6	36.2	32.2	33.6	24.8	-07	-23
			25.8	23.0	16.6	10.6	-36	-54
26.4			22.2	22.0	12.2	-17	-45	
Average.				-20	-41			
Rotation of environment only	Rotation alternately clockwise and counter-clockwise	7	29.2	29.4	22.0	17.0	-25	-42
			19.6	18.2	16.4	17.8	-16	-02
			24.0	19.8	21.8	24.6	-09	+24
			Average.				-17	-07
	Rotation in clockwise direction only	8	27.0	26.0	29.6	19.4	+10	-25
			26.6	27.8	24.6	16.4	-08	-41
19.0			27.4	16.8	14.8	-12	-46	
Average.				-03	-37			

in Groups 1 and 2, i.e., in those birds subjected to actual bodily rotation with vision eliminated. It will also be noted that under these conditions the reductions produced in the clockwise and the counter-clockwise post-rotational nystagmus by practice in the clockwise direction only are equal and that the same is also true of the reductions produced by practice alternately in the clockwise and counter-clockwise directions. Moreover, it is to be noted that these two sets of reductions are also equal to each other.

The results produced by the repeated rotation of Groups 3 and 4, with vision permitted, indicate, despite considerable irregularity in particular instances, that little or no real reduction in the purely vestibular nystagmus has been produced by either the exclusively clockwise or alternately clockwise and counter-clockwise rotation practice. This finding, more clearly portrayed by subsequent experiments, was wholly unexpected and has presumably not been previously reported.

The repeated rotation of the birds in both Group 5 and Group 6 seemed to have a tendency to reduce the counter-clockwise after-nystagmus more than the clockwise after-nystagmus. However, as later experiments will show, this tendency was due merely to chance variables.

The difference in the amount of reduction shown by the birds in Group 7 for the clockwise and counter-clockwise directions is, again, probably not reliable. However, the difference shown in this respect by the birds in Group 8 is reliable, as will be brought out in a later series.

The results obtained from this preliminary series of experiments made it evident that in future experiments the testing procedure would have to be altered so as to increase the reliability of the nystagmic measures. Certain expedients were adopted in this connection which will be made apparent in the description of the following series of experiments.

Series B

In this series of experiments, 24 previously unrotated pigeons were tested, on April 18, for clockwise and counter-clockwise

post-rotational nystagmus in exactly the same manner as in the preceding experiment except that the rate of rotation used was one revolution in one and one-half seconds instead of one revolution in two seconds. Then on April 19, the birds were all again tested in the same manner, except that they were rotated in the

TABLE 2

Post-rotational nystagmus times of 24 previously unrotated pigeons (Series B)

GROUP	CLOCKWISE			COUNTER-CLOCKWISE		
	April 18	April 19	Average	April 18	April 19	Average
	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>
1	23.0	24.6	23.8	17.6	27.8	22.7
	21.8	25.8	23.8	22.8	23.6	23.2
	21.4	23.8	22.6	20.8	23.0	21.9
	21.6	24.0	22.8	22.0	21.2	21.6
	24.2	19.8	22.0	15.6	33.6	24.6
	20.4	18.6	19.6	20.2	23.0	21.6
2	28.4	28.6	28.5	23.2	24.4	23.8
	15.8	21.2	18.5	13.4	23.6	18.3
	19.8	20.8	20.3	14.0	20.6	17.3
	28.2	25.0	26.6	19.6	27.0	23.3
	18.0	24.4	21.2	17.2	23.4	20.3
	21.2	26.8	24.0	17.6	27.8	22.7
3	23.8	31.2	27.5	11.6	28.4	20.0
	23.4	32.8	28.1	16.0	35.0	25.5
	37.8	33.6	35.7	33.6	34.0	33.8
	11.4	15.6	13.5	10.2	19.8	15.0
	30.0	21.8	25.9	24.8	27.4	26.1
	27.4	28.4	27.9	26.6	24.4	25.5
4	22.0	23.8	22.9	26.4	22.0	24.2
	29.4	21.0	25.2	25.4	24.8	25.1
	21.6	20.0	20.8	18.4	26.8	22.6
	24.8	30.6	27.7	25.0	23.6	25.3
	18.0	20.2	19.1	15.0	17.0	16.0
	27.0	37.4	32.2	15.0	27.4	21.2

counter-clockwise direction first and then in the clockwise direction rather than in the reverse order. The nystagmus times obtained on these four individual rotation tests and the average nystagmus time for each bird for the two clockwise and two counter-clockwise tests are given in table 2.

TABLE 3

Percentage of change in the post-rotational nystagmus times of 24 pigeons after 24 and after 36 days of habituation to repeated rotation under the conditions indicated by the legends in the left-hand column

	GROUP	24-DAY TEST		36-DAY TEST	
		CW	CCW	CW	CCW
Rotation of body only. Vision ex- cluded	1	<i>per cent.</i>	<i>per cent.</i>	<i>per cent.</i>	<i>per cent.</i>
		-67	-38	-45	-49
		-70	-42	(Became ill)	
		-66	-55	-63	-60
		-51	-55	-54	-40
		-71	-67	-37	-09
		-49	-51	-49	-52
		Average. . .	-62	-55	-50
					-42
Rotation of body only. Vision per- mitted	2	-12	+19	+06	+33
		+12	+25	+49	+42
		00	+40	-21	-13
		-29	-40	-20	-13
		+20	-12	+24	-05
		+25	-23	+28	-31
		Average. . .	+03	+02	+02
Rotation of body and environment	3	-27	+17	-20	+18
		-37	-24	-20	-17
		-53	-37	-25	-38
		00	+25	-07	+22
		-19	-38	-04	-21
		+05	-08	-28	-18
		Average. . .	-22	-11	-17
					-09
Rotation of environment only	4	-13	-35	-07	-32
		+12	-22	-04	-34
		-13	-25	-09	-23
		+10	-11	-01	-19
		+01	-09	+14	-09
		+09	+04	+04	-01
		Average. . .	+01	-16	-01
					-20

These 24 birds were then arbitrarily divided into four groups of six birds each. Beginning on April 20, each of these four groups was daily subjected to ten periods of rotation under one of the four conditions indicated by the legends in the left-hand column of table 3. The speed of the practice rotation was the same as used in the testing of these birds, namely, one revolution in one and one-half seconds; and the successive rotation periods lasted 30 seconds, with interpolated rest periods of the same duration. Groups 1, 2, and 3 were practiced only in the clockwise direction. In the case of Group 4, however, the environment was rotated exclusively in the counter-clockwise direction.

At the end of 24 days of practice rotation, each of the 24 birds comprising the four groups just described was tested for vestibular nystagmus in exactly the same manner as before the habituation had been commenced. The percentage of change in the clockwise and counter-clockwise nystagmus time for each bird is given in the two columns, headed "24-day test," in table 3.

Immediately following this first re-test, the four groups of pigeons were subjected to twelve days of further habituation under the same conditions as those to which they had formerly been subjected. A second re-test, following this second period of habituation, indicated that no consistent change had been produced by the additional habituation, but afforded verification of the reliability of the results obtained on the first re-test (see the two columns, headed "36-day test," in table 3).

The nystagmus reduction produced in Group 1 of the present series, it will be noted, is quite comparable to the reduction produced under similar conditions in Group 2 in Series A. On the basis of these combined findings, it may be concluded that repeated bodily rotation in only one direction, with vision excluded and with the successive periods of rotation and rest of equal duration, produces an equal reduction in the duration of the after-nystagmus elicited by bodily rotation in both the clockwise and in the counter-clockwise directions. It is further evident that an average reduction of about 60 per cent in the duration of the post-rotational nystagmus is probably the maximal effect which can be produced under the conditions just described.

The results obtained from Group 2 in the present series confirm the results obtained from Groups 3 and 4 in Series A: repeated bodily rotation under the conditions of the present series, with vision permitted, produces no reduction whatever in the duration of the nystagmus elicited by bodily rotation with vision excluded.

The birds in Group 3 showed a relatively greater reduction in post-rotational nystagmus for the direction of practice than for the opposite direction of rotation. However, since the amount of difference here is slight and since exactly the opposite tendency was observed in the results obtained from Group 6 in Series A, it seems probable that the differences noted in the two instances were entirely non-significant, that is to say, that the reduction of purely vestibular nystagmus which is produced by repeated rotation of the subject and environment simultaneously is about equal for both the clockwise and counter-clockwise after-nystagmus and is, furthermore, considerably less pronounced than the reduction produced by repeated bodily rotation with vision eliminated.¹³

The results obtained from the six birds in Group 4 reveal that the repeated rotation of the environment in the counter-clockwise direction produces no noticeable modification in the vestibular after-nystagmus for the clockwise direction of bodily rotation but does produce a slight and fairly consistent reduction in the after-nystagmus for the counter-clockwise direction of rotation. That this differential effect is reliable is further indicated by the fact that strictly comparable results were obtained from the three birds in Group 8 in Series A. In passing, it may be pointed out that the nystagmus elicited by counter-clockwise rotation of the environment is identical, as regards the respective directions of the

¹³ It should be mentioned at this point that it was impossible to accelerate or retard the cylinder comprising the artificial environment of the rotation apparatus used in the present investigation in less than five seconds. Since this slower rate of acceleration and retardation was unavoidably used in the repeated rotation of the birds in Groups 5 and 6 in Series A and in Group 3 in the present series, it is impossible, therefore, to make a close comparison of the habituation effects thereby produced with the habituation effects produced by the rotation of subjects with the environment stationary.

slow and quick components of the response, with the vestibular after-nystagmus elicited by counter-clockwise bodily rotation. This fact is in some way responsible, no doubt, for the results just cited; but it is impossible at the present time to determine the exact manner in which the observed effects were produced.

Series C

In this series, 24 previously unrotated pigeons were tested for vestibular after-nystagmus on two successive days, May 16 and 17, in exactly the same manner as described for the 24 birds used in Series B. The nystagmus time for each bird for the four periods of rotation and the average nystagmus time for the two clockwise and two counter-clockwise periods are given in table 4. Again the 24 birds were divided into four equal groups. The birds in Group 1 of this series were subjected to the same general routine of repeated bodily rotation as was used in Series B, with this variation, however, that the head of each bird was held in a fixed position with reference to the rest of the bird's body during the repeated rotation (see illustration 4 in plate 2). Moreover, vision was uniformly excluded throughout the rotation practice. Under these conditions there was a decided and roughly equal reduction for both the clockwise and the counter-clockwise after-nystagmus, as indicated in table 5.

Group 2 in this series was subjected to the same schedule of repeated rotation as Group 1, also with head fixed, but with vision permitted (see illustration 3 in plate 2). Under these conditions there was a conspicuous reduction in the clockwise after-nystagmus but no significant change in the counter-clockwise after-nystagmus.

The birds in Group 3 were subjected to the repeated rotation with the head free and vision excluded, but were unique in that they were rotated for only 6 seconds and rested for 54 seconds instead of being rotated and rested for equal intervals of 30 seconds, as were all previous groups. The results for this group are given in table 5 and confirm Holsopple's contention that the relative duration of the rotation and rest intervals is an important factor in determining whether the clockwise or counter-clockwise

after-nystagmus will be the more markedly reduced by rotation practice in a given direction.

The birds in Group 4 were subjected to the same experimental conditions as the birds in Group 3, except that they were rotated

TABLE 4
Post-rotational nystagmus times of 24 previously unrotated pigeons (Series C)

GROUP	CLOCKWISE			COUNTER-CLOCKWISE		
	May 16	May 17	Average	May 16	May 17	Average
1	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>	<i>seconds</i>
	26.4	18.0	22.2	21.6	19.2	20.4
	19.2	16.2	17.7	15.6	20.2	17.9
	15.6	23.8	19.7	12.8	35.0	23.9
	21.0	19.0	20.0	18.6	19.8	19.2
	21.4	19.6	20.5	19.0	20.0	19.5
	28.8	27.2	28.0	23.0	34.0	28.5
2	24.8	27.6	26.2	17.8	22.0	19.9
	37.0	34.6	36.8	37.8	41.0	39.4
	21.8	19.4	20.6	14.4	14.2	14.3
	24.4	24.6	24.5	28.0	25.0	26.5
	27.2	22.0	24.6	28.0	28.0	28.0
	11.8	19.4	15.6	14.8	19.2	17.0
3	28.0	22.2	25.1	18.6	20.0	19.3
	29.4	24.4	26.9	26.2	23.8	25.0
	31.6	31.8	31.7	27.2	31.6	29.4
	26.0	26.8	26.4	22.8	17.6	20.2
	26.4	29.2	27.8	23.0	20.8	21.9
	41.0	39.0	40.0	37.2	34.4	35.8
4	22.2	20.0	21.1	20.4	21.8	21.1
	19.6	20.6	20.1	22.0	19.6	20.8
	17.0	24.4	20.7	16.6	20.4	18.5
	27.6	24.4	26.0	29.6	37.2	33.4
	29.8	28.6	29.2	22.8	26.4	24.6
	26.0	30.6	28.3	29.0	31.8	30.4

for 54 seconds and rested only 6 seconds. Under these conditions, it will be noted from the results presented in table 5, that the reduction of the clockwise and counter-clockwise post-rotational nystagmus is about equal. According to Holsopple's hypothesis, the counter-clockwise after-nystagmus should have been more

TABLE 5

Percentage of change in the post-rotational nystagmus times of 24 pigeons after 24 and after 36 days of habituation to repeated rotation under the conditions indicated by the legends in the left-hand column

	GROUP	24-DAY TEST		36-DAY TEST	
		CW	CCW	CW	CCW
Head fixed. Vision excluded	1	<i>per cent.</i>	<i>per cent.</i>	<i>per cent.</i>	<i>per cent.</i>
		-64	-49	-60	-50
		-34	-23	-16	-05
		-32	-32	-22	-25
		-25	-24	+09	+09
		-74	-64	-51	-51
		-64	-36	-35	-34
	Average...	-47	-38	-29	-26
Head fixed. Vision permitted	2	00	+24	-58	+40
		-67	00	-66	-02
		-58	+22	-65	-12
		-19	+05	-59	-24
		-58	-15	-54	-35
		-23	+11	-38	+02
	Average...	-38	-08	-57	-05
Rotation-rest ratio: 6 sec- onds: 54 sec- onds	3	-65	+02	-39	-25
		-28	-12	-34	-32
		-54	-26	-28	-27
		-31	+18	-28	+19
		-44	-08	-18	+05
		-40	-31	-36	-13
	Average...	-44	-10	-31	-12
Rotation-rest ratio: 54 sec- onds: 6 sec- onds	4	-60	-56	-52	-51
		-15	-43	-27	-29
		-24	-11	-20	-04
		(Escaped)			
		-49	-47	-45	-33
		-53	-60	-41	-61
	Average...	-40	-43	-37	-40

markedly reduced in consequence of this practice schedule than the clockwise after-nystagmus. The probable reason why this did not occur is that, although the clockwise after-nystagmus was prevented from "running to normal completion" during the successive periods of rotation within a given session, this response was unavoidably permitted to run to "normal to completion" once at the end of each session. It is quite likely, therefore, that if the clockwise and counter-clockwise after-nystagmus of the birds in this group had been tested, say, at the end of five or six days' practice, the counter-clockwise after-nystagmus would have shown an appreciably greater reduction than the clockwise after-nystagmus. However, since the nystagmus was not tested until after 24 days of habituation, it may be assumed that, by virtue of the unavoidable situation just referred to, the clockwise as well as the counter-clockwise after-nystagmus had been permitted to run their full course sufficiently often for them *both* to have reached maximum habituation for the given conditions.

In addition to the results which have already been described, certain incidental observations were made which seem worth reporting. In Series A motion picture records were made of both the rotational and post-rotational nystagmus of certain birds in Groups 1 and 2, both before and after the habituation period. These records showed that the rotational and post-rotational nystagmus for both the clockwise and counter-clockwise directions were equally reduced by the conditions of rotation practice to which the birds in these two groups were subjected. This finding is in opposition to the findings of Maxwell (53) and of Pilz (61) which were mentioned on a previous page. As suggested at that time, the presence of vision during the habituation experiments of these latter investigators was probably responsible for the difference in the degree of reduction observed by them in the nystagmus occurring during rotation and in the so-called after-nystagmus.

Careful observation of the birds comprising Groups 3 and 4 in Series A and Group 2 in Series B revealed that when pigeons are rotated with vision permitted, there is a vigorous nystagmus

during the entire period of rotation with little or no after-nystagmus when rotation is ended (cf. Mowrer (58)). It was further observed that these relations were not noticeably altered by extensive repetition.

Motion pictures were made of some of the birds in Groups 5 and 6 in Series A, which were subjected to the repeated bodily rotation with the environment rotating concurrently. These motion picture records showed that at the onset of the practice rotation, there was usually a conspicuous though brief nystagmus produced by acceleration and a comparable nystagmus produced by retardation. As the practice rotation proceeded, however, both of these responses gradually disappeared. This finding was confirmed by direct observation of the birds comprising Group 3 in Series B.

At the onset of the habituation of the birds in Groups 7 and 8 in Series A and Group 4 in Series B, it was frequently noted that the nystagmus elicited by the rotation of the environment often persisted for four or five seconds after the environment had been brought to complete rest. This persistence of visually elicited nystagmus after the stopping of the environment has been dealt with independently in another paper (57) and need not be discussed here except to mention that this type of after-response gradually disappeared as the repeated rotation of the environment was continued from day to day. There was, however, no noticeable weakening in the nystagmus elicited during the actual rotation of the environment.

VI. SUMMARY

Previous investigations have been reviewed which indicate that the nystagmus produced by bodily rotation may often be significantly reduced, in both duration and magnitude, by means of repeated elicitation. An analysis of the experimental conditions employed by the various investigators in this field has revealed that a variety of factors may be influential in determining the rate and extent of nystagmus reduction produced by any given schedule of repeated rotation. Different investigators have allowed these factors to operate in their respective experiments in a wide variety of controlled (and uncontrolled) ways, with the

result that inconsistencies and contradictions in previously published data have frequently obscured genuine cause-and-effect relationships and have made an understanding of this "habituation" phenomenon and the conditions conducive to its occurrence extremely difficult.

Conspicuous among the reasons for this confused state of affairs is the failure of certain writers to differentiate clearly between *vestibular nystagmus*, i.e., nystagmus produced by angular acceleration or retardation, or by certain other physical agencies (notably heat and electricity) which are known to have a stimulating effect upon the sense organs of the non-acoustic labyrinth, and *visual nystagmus*, i.e., nystagmus produced by movement of the visual environment with reference to the subject or by movement of the subject with reference to the visual environment. Both of these types of nystagmus are identical in that they consist of an oscillatory pattern of head or (in some species, including human beings) eye movements, involving a slow, "compensatory" drift in one direction alternating with a quick, "saccadic" response in the opposite direction. Under ordinary biological conditions, the reflexes responsible for vestibular and visual nystagmus function harmoniously and complementarily; but under experimental conditions, these two types of response tendency are often mutually antagonistic. In any attempt to analyse the conditions and factors favoring the habituation of the nystagmus occurring either during or after bodily rotation, it is therefore highly imperative that the visual and vestibular elements involved in any given experimental situation should be fully recognized and controlled.

Another point which must be taken into full account is that for any given plane of head (or eye) movement, there can be two and only two patterns of nystagmic response, regardless of whether the reactions are elicited by visual or by vestibular stimulation alone or in combination. Thus, in the case of *horizontal nystagmus*, there may be a *nystagmus to the right* or a *nystagmus to the left*, the particular designation depending, by arbitrary agreement, upon the direction of the *quick* component of the response with reference to the subject. The *vestibular*

nystagmus produced by bodily acceleration in the clockwise direction and by retardation in the counter-clockwise direction is, in this conventionally accepted terminology, a *nystagmus to the right*; and, conversely, the vestibular nystagmus produced by bodily acceleration in the counter-clockwise direction and by retardation in the clockwise directions is a *nystagmus to the left*. Likewise, the *visual nystagmus* produced by rotation of the visual environment in the counter-clockwise direction (to the left) with reference to the subject or by rotation of the subject in clockwise direction with reference to the environment is a *nystagmus to the right*; and, conversely, the visual nystagmus produced by rotation of the visual environment in the clockwise direction (to the right) with reference to the subject and by rotation of the subject in the counter-clockwise direction with reference to the environment is a *nystagmus to the left*.

With the foregoing relationships and definitions presupposed, the conclusions summarily stated below and based upon a series of habituation experiments described in the preceding section of this paper seems justifiable, it being understood, however, that these conclusions are not necessarily valid for any type of subject other than the type used in this investigation (namely, pigeons) and that all use of the term *nystagmus* will refer exclusively to *head nystagmus*, in the horizontal plane.

1. With the subject's vision excluded and the successive rotation and rest intervals of equal and fairly long duration, repeated bodily rotation in either the clockwise or counter-clockwise direction or alternately in both directions may be relied upon to produce a substantial and equal diminution in both the rotational (acceleration) and post-rotational (retardation) vestibular nystagmus for both directions of turning.

2. If the conditions described in 1 are varied so as to make the rest (retardation-to-acceleration) interval longer than the rotation (acceleration-to-retardation) interval, repeated bodily rotation in a given direction tends to produce a *greater* reduction in the post-rotational nystagmus for the direction of practice (and in the rotational nystagmus for the unpracticed direction) than in the post-rotational nystagmus for the unpracticed direction (and

in the rotational nystagmus for the practiced direction). (This statement is probably true only within limits: thus, if the duration of the successive periods of rotation equals or exceeds the duration of the rotational nystagmus, the differential effect just described cannot be expected to occur.)

3. If, on the other hand, the conditions described in 1 are varied so as to make the rotation interval longer than the rest interval, repeated bodily rotation in a given direction tends to produce a *smaller* reduction in the post-rotational nystagmus for the direction of practice (and in the rotational nystagmus for the unpracticed direction) than in the post-rotational nystagmus for the unpracticed direction (and in the rotational nystagmus for the direction of practiced), although the unavoidable occurrence of an indefinitely long rest period at the end of each session of repeated rotation tends to make the difference in the reduction of the two types of nystagmus less conspicuous than the difference usually obtained under the conditions described in 2. (This statement, like 2, is probably true only within limits: thus, if the duration of the rest intervals interpolated between the successive rotation intervals equals or exceeds the duration of the post-rotational nystagmus, the differential effect just described cannot be expected to occur.)

4. The particular propositions posited in 1, 2, and 3 may be stated generally, as follows: The longer a given type of vestibular nystagmus is allowed to persist, uninterrupted by an opposing vestibular stimulus, the greater the likelihood that repeated elicitation will reduce the duration and magnitude of this response. (This proposition, previously stated in somewhat different terms by Holsopple (38), should, however, be regarded merely as a descriptive, not as an explanatory concept.)

5. Although vestibular nystagmus may be substantially reduced (about 60 per cent on the average) by means of repeated elicitation with vision excluded, this response cannot, however, be abolished (except, perhaps, at intensities of stimulation considerably weaker or stronger than employed in the present investigation).

6. When the type of subject used in this investigation is rotated

with vision permitted, there is a vigorous nystagmus during the entire rotation period but little or no post-rotational nystagmus; repeated bodily rotation either in the clockwise or in the counter-clockwise direction or alternately in both directions does not perceptibly modify this pattern of response.

7. Repeated bodily rotation under the conditions described in 6 likewise does not affect either the rotational or post-rotational vestibular nystagmus produced by bodily rotation in either direction with vision excluded.

8. When bodily rotation is accompanied by concurrent rotation of the visual environment, there is a slight (acceleration) nystagmus at the onset of rotation and a slight (retardation) nystagmus at the end of rotation, both of which responses gradually disappear with repeated elicitation.

9. Repeated bodily rotation under the conditions described in 8, either in the clockwise or in the counter-clockwise direction or alternately in both directions, produces a slight (about 20 per cent on the average) and equal reduction in the vestibular nystagmus elicited during and after rotation in either direction with vision excluded.

10. Rotation of a visual environment around a stationary subject produces a vigorous nystagmus which lasts as long as the rotation of the environment is continued (or until the subject is fatigued) and which tends to persist for a brief time after the environment has been brought to rest; this persistence of the visually elicited nystagmus after the environment has been stopped gradually disappears with repetition.

11. Repeated elicitation of visual nystagmus under the conditions described in 10, with the successive rotation and rest intervals of equal duration, produces a decided reduction (about 50 per cent on the average) in the post-rotational vestibular nystagmus elicited by bodily rotation in the same direction as the repeated rotation of the environment but does not perceptibly modify the post-rotational vestibular nystagmus elicited by bodily rotation in the opposite direction.

12. Repeated bodily rotation in a given direction with vision permitted and head held in a fixed position with reference to the

body produces a significant reduction (about 45 per cent on the average) in the post-rotational vestibular nystagmus elicited by bodily rotation in the practiced direction but does not modify the post-rotational vestibular nystagmus elicited by rotation in the opposite direction.

13. Repeated bodily rotation in a given direction, with vision excluded and head held in a fixed position with reference to the body produces a significant (about 35 per cent on the average) and equal reduction in both the clockwise and counter-clockwise post-rotational vestibular nystagmus.

14. Repeated bodily rotation under the conditions described in 13 thus produces less reduction in both types of post-rotational vestibular nystagmus than does similar rotation with the head free (cf. 5).

The supposition that the reduction of vestibular nystagmus by means of repeated elicitation may be dependent upon injury to or structural modification of the vestibular receptors has been disproved by a variety of experiments which have been reviewed elsewhere (22), (59). The reduction process, whatever its specific nature may be, must, in all probability, occur somewhere within the central nervous system. This conclusion is consistent with the theory that the persistence of vestibular nystagmus after the cessation of actual physical stimulation is mediated by the action of a mechanism located within the central nervous system. On the other hand, this conclusion, as well as the experimental facts cited in the immediately preceding pages, is opposed to the notion that the reduction of vestibular nystagmus by means of repeated elicitation is dependent upon "fatigue" or upon "sensory adaptation" of the type characteristic of vision, taste, smell, and certain other sensory mechanisms.

Since vestibular nystagmus is a useless, mal-adaptive response under the experimental conditions in which it is most readily habituated, it has been suggested that the habituation may be dependent upon a learning process, fundamentally similar to the process involved in the elimination of other useless or harmful responses (Abels (1), Dodge (14)).

Since the conditions under which vestibular nystagmus is most

readily habituated are seldom or never encountered by most living organisms in their ordinary existence, it has been suggested that the habituation of this response may be dependent upon a breakdown or dissociation of normal, integrated functioning and may therefore represent a pathological rather than an adaptive type of process (Abels (1)).

So far as can be seen at the present time, none of the findings of this or any other investigation previously reported provides definitive, or even strongly presumptive, evidence in favor of either of the hypotheses just stated; but the experimental facts now available do seem to suggest that one or the other of these hypotheses is probably the correct explanation of the modifiability of vestibular nystagmus by means of repeated elicitation.

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